Black noise and population persistence

Kim M. Cuddington[*] and Peter Yodzis

Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Biological populations are susceptible to random variation in environmental influences such as temperature and moisture. This variability (or noise) can determine population size and, ultimately, cause extinctions. Extinction risk depends on noise colour or the amount of short- and long-term variation. Most environmental noise is reddened: the variation is dominated by long-term fluctuations. Recent modelling has shown that moderately reddened noise affects populations differently from the white noise used in earlier studies. However, some geophysical phenomena, such as temperature and river height, can have deeply reddened 'brown' or even 'black' spectra. We find that, compared to environments characterized by red noise, very long population persistence times are more likely for black noise. Unlike previous work incorporating a simple autoregressive model of reddened noise, our model suggests that the large variation associated with persistence in a red-noise environment limits our ability to predict the fate of particular populations subject to this noise colour. Thus, we identify the colour of noise experienced by a population—red or black—as a crucial factor in any attempt to manage or conserve that population.

Keywords: extinction risk; noise colour; persistence

1. INTRODUCTION

Environmental variation can be characterized by features such as magnitude of variation and noise colour. Noise colour refers to the partitioning of variation in time-series data. In a spectral analysis, the time-series of some environmental characteristic, such as temperature, is described as a set of sine waves with different frequencies and the variance associated with each frequency is determined. White noise gets its name from an analogy to white light, as it contains an equal mix of all frequencies. Coloured noises have a preponderance of frequencies of a given range. If a time-series is dominated by long-term cycles, the noise is called reddened, again by analogy to red light.

Earlier work examining the effect of environmental noise on populations used white noise as a model of environmental variation (May 1973; Lande 1993), but we now know that most environmental noise contains long-term fluctuations (Mandelbrot & Wallis 1969; Steele 1985; Warner *et al.* 1995). In particular, it has been suggested that the variability of a wide range of natural phenomena is well described by $1/f^\beta$-type noises (Halley 1996), where variance at each frequency scales according to a power law. The value of the spectral exponent β indicates the noise colour. Red (or pink) noise ($\beta = 1$) has been recommended as a better null model of environmental variation than white noise ($\beta = 0$) (Halley 1996). Although $1/f^\beta$ noise may be a good model for environmental noise, not all reddened noise is red. Geophysical variables are described by a range of spectral exponents from red to black noise (table 1). For example, river height and marine temperature fluctuations may be best described as brown ($\beta = 2$) to 'black' noise ($\beta = 3$) (Schroeder 1991).

Lawton (1988) speculated that the probability of population extinction may increase with reddened noise, since the temporal correlation makes it more likely that a run of bad conditions may occur. Previous authors have found that extinction risk is actually determined by complex relationships between noise colour, variance and underlying dynamics (Johst & Wissel 1997; Halley & Kunin 1999; see also the review by Kaitala *et al.* (1997)). For example, Ripa & Lundberg (1996) and Petchey *et al.* (1997) found that reddened noise increased persistence where dynamics were overcompensatory, and decreased persistence for populations with undercompensatory dynamics. Almost all earlier studies have only considered moderately reddened noise ($\beta = 0$–1.5) generated by a simple autoregressive process (however, see Halley & Kunin 1999).

It is unlikely that either an autoregressive function or a $1/f^\beta$ model describes all noise signals. However, simple autoregressive models cannot produce noise colours darker than brown and do not produce a true $1/f^\beta$ spectrum for red noise. The variance of time-series data generated by an autoregressive function quickly increases to some finite value (Halley 1996), rather than according to a power law and, consequently, long-term fluctuations contribute less variance to the total signal (figure 1). Therefore, even when the mean, variance and estimated noise colour are the same, autoregressive and $1/f^\beta$ noise have quite different characters. We incorporated reddened noise, modelled using either a simple autoregressive function or a $1/f^\beta$ noise function over a larger range of noise colours, into the single-species population model used by Petchey *et al.* (1997).

2. POPULATION AND NOISE COLOUR MODELS

Single-species population dynamics were modelled using a modified Ricker equation from previous studies

[*]Author for correspondence (kcudding@uoguelph.ca).

969

Table 1. *Range of spectral exponents found in geophysical data*

environmental characteristic (location or source)	length of scaling interval	spectral exponent	reference
earthquake frequency (Appenes, Italy)	ten years	0.34	Lapenna *et al.* (1998)
mean monthly temperature (average of 94 stations)	*ca.* 85 years	0.43	Pelletier (1997)
mean daily relative air humidity (Balaton, Hungary)	26 years	0.61	Vattay & Harnos (1994)
mean daily temperature (mean of 1000 continental stations)	one month	1.37	Pelletier (1997)
monthly temperature (Northern hemisphere)	100 years	1.80	Lovejoy & Schertzer (1986)
annual temperature (inferred from Vostok ice core)	2–40 kyr	2.00	Pelletier (1997)
temperature (s^{-1}), anchored location (St Lawrence Estuary)	*ca.* 4.5 h	2.30	Currie (unpublished data)
annual precipitation (Baltimore, USA)	145 years	2.50[a]	Mandelbrot & Wallis (1969)
annual minima (Nile River)	847 years	2.82[a]	(Mandelbrot & Wallis (1969)

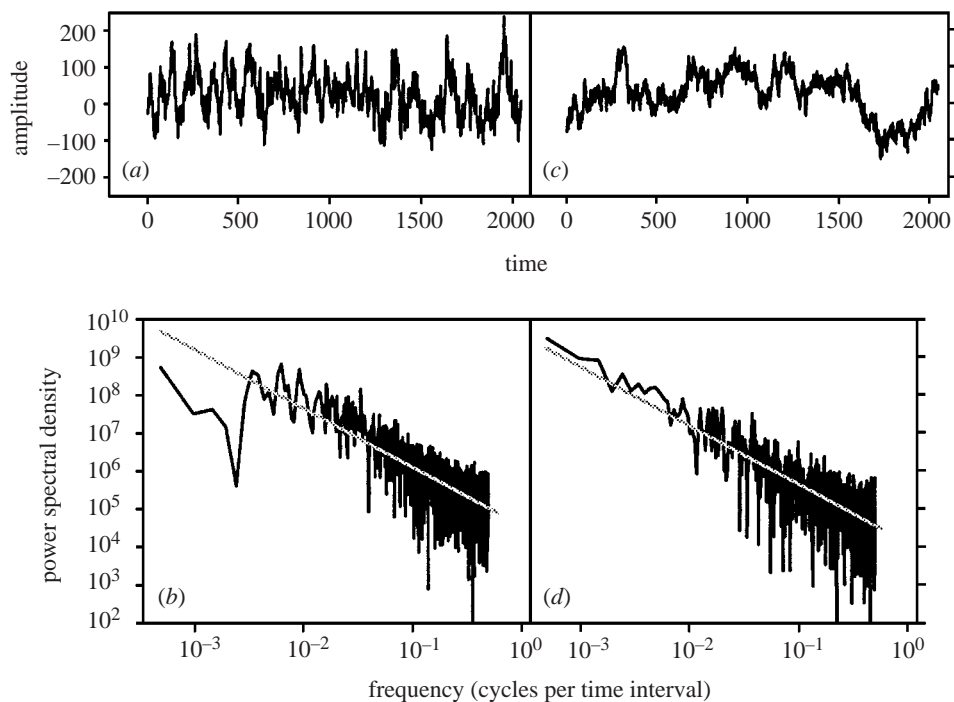[a] Calculated from the Hurst exponent.

Figure 1. (*a*) and (*c*) Noise time-series $(\phi_1, \ldots, \phi_{2048})$ and (*b*) and (*d*) spectral density of reddened noise generated using either (*a*) and (*b*) a simple autoregressive process or (*c*) and (*d*) a spectral synthesis function which generates $1/f^\beta$ noise. The mean and variance for the data are identical. The grey line shows the slope of the linear regression: (*b*) autoregressive noise $= -1.575$ and $r^2 = 0.58$ and (*d*) $1/f^\beta$ noise $= -1.579$ and $r^2 = 0.54$.

(Petchey *et al.* 1997), where demographic stochasticity was included by drawing the population size at a given time (N_t) from a Poisson distribution, $\mathcal{Z}$, with the mean given by the expectation from the population model as

$$N_t = \mathcal{Z}\left[N_{t-1}\exp\left(r\left(1 - \frac{N_{t-1}}{K_t}\right)^\gamma\right)\right],$$

where $N_0 = K_0 = 100$. The degree of over- or undercompensation is given by the exponent γ, where γ ranges from 0 to 1 and $\gamma = 1$ indicates overcompensation. A low reproductive rate $(r = 1.5)$ was used to generate population dynamics with a stable point attractor.

Environmental noise was included in the carrying capacity (K). At each time-step, K was given as

$$K_t = K_0 + \phi_t,$$

where ϕ_t was drawn from either an autoregressive noise function or a $1/f^\beta$ noise function and $K_0 = 100$. The carrying capacity was restricted to positive values: where ϕ_t generated a negative value, K_t was set to 5. Population extinction occurred when $N_t < 1$ and, where extinction occurred during the simulation, the persistence time was defined as t. When extinction did not occur, the persistence time t was set to the maximum length of the simulation. The mean and variance for persistence times were calculated for 500 simulations, run for a maximum duration of 200 000 generations, where populations that did not persist for more than one time-step were excluded.

The autoregressive function was given as

$$\phi_t = \alpha\phi_{t-1} + \rho\varepsilon_t,$$

as in previous studies (Ripa & Lundberg 1996; Petchey *et al.* 1997), where ε_t is a random number drawn from a normal distribution with zero mean and unit variance and α ranges from 0 to 1 and gives the degree of temporal autocorrelation. The variance of the signal is determined by ρ, where

$$\rho = 70(1 - \alpha^2)^{1/2},$$

as in Petchey *et al.* (1997).

$1/f^\beta$ noise with spectral exponents ranging from 0 to 3.2 was generated using a spectral synthesis approximation. In this method, amplitudes and periods of the desired spectral exponent are generated and sent to an inverse fast Fourier transform (Saupe 1988; Voss 1988). To produce a time-series signal with a given spectral exponent, N random phases, $\theta_1, \ldots, \theta_N$, uniformly distributed on $[0, 2\pi]$ and N normally distributed random numbers, with zero mean and unit variance, $\varepsilon_1, \ldots, \varepsilon_N$, were generated. For $1/f^\beta$ noise, the amplitudes of the components are coupled to their frequencies via a power law; as the scale of the components decreases, their amplitudes decrease at a rate determined by the spectral exponent. Therefore, to generate the amplitudes for a given spectral exponent, each normally distributed number (ε_f) is multiplied by $1/f^{\beta/2}$ to form the amplitudes a_f. The complex coefficients are calculated as

$$a_f \exp(i\theta_f) \equiv a_f \cos\theta_f + ia_f \sin\theta_f$$

and the inverse fast Fourier transform of the coefficients is taken. The real part of the resulting sequence is used to form the temporal noise series $\tau_1, \ldots, \tau_N$ (Saupe 1988; Voss 1988; Hastings & Sugihara 1993).

Since the spectral synthesis method generates a periodic sequence (Saupe 1988), where variance only increases to $N/2$, N was set to 524 288 (2^{19}) and only the first 200 000 numbers were used. Sequences $\tau_1, \ldots, \tau_N$, generated using spectral exponents (β) greater than one, may have non-stationary means but have finite variance over a finite duration. The mean and variance of the temporal noise sequence $\tau_1, \ldots, \tau_M$, where $M = 200\,000$, were determined and used to generate a standardized $1/f^\beta$ noise sequence, $\phi_1, \ldots, \phi_M$, with zero mean and variance of 4140, to enable comparison with Petchey *et al.* (1997).

Noise colours for autoregressive and $1/f^\beta$ noise time-series used with the population model were estimated from a linear regression of the power spectra of the synthesized noise, where f ranged from 1 to 131 072 (2^{17}). The power spectra were generated without a smoothing window. In practice, standardized temporal series of length M, generated via spectral synthesis, had spectral exponents somewhat smaller than the value used to create the series.

3. RESULTS AND DISCUSSION

We found that a $1/f^\beta$ noise model makes considerably different predictions than those of an autoregressive noise model. Overall, the $1/f^\beta$ noise model predicts that darker noise increases mean population persistence time (figure 2a). These findings agree with Halley & Kunin's (1999) work comparing the extinction probabilities of white, red and brown population time-series. For populations with overcompensatory dynamics, there is a dramatic increase in population persistence with darker noise. Brown to black noise ($\beta > 2$) produces very long mean persistence times compared to less reddened noise ($\beta = 0.5{-}1.5$). The long mean persistence times of populations in a black environment are very robust with respect to the form of the underlying model. There is no effect of under- or overcompensatory dynamics on the mean persistence time in the darker regions of the spectra (figure 2a). In contrast, when environmental variation is modelled using an autoregressive process, the mean persistence time decreases with noise darkness for undercompensatory dynamics and increases for overcompensatory dynamics, as found by Petchey *et al.* (1997) (figure 2b).

The coefficient of variation (CV) of the persistence time indicates how reliable the mean is as an estimate of population persistence. For autoregressive noise, the CVs vary little among most parameter combinations (about 1.0), but approach zero where most populations persist for the entire simulation (figure 2d). In comparison, the CVs are functions of noise colour and dynamics for the model incorporating $1/f^\beta$ noise (figure 2c). The CVs are very large (1.6–2.3) for moderately reddened noise ($\beta = 0.5{-}1.5$), indicating that the ultimate effect of a red environmental noise on population persistence is quite unpredictable. The same pattern of variability is also found for simulations with a much shorter duration (200 generations).

The large variation associated with red noise generated by a $1/f^\beta$ process (figure 2c) may have a simple explanation. Although white noise has an equal mixture of high and low frequencies, the influence of short cycles on the total signal is much greater than the influence of long-term cycles. Similarly, darker noises ($\beta > 1.5$) are dominated by the much greater influence of long cycles. Red noise has a balanced influence on both short- and long-term cycles (Keshner 1982). Consequently, many interactions between the effects of short and long cycles are possible in red noise signals and may strongly affect the total signal. Long-term trends can reinforce a short-term cycle or ameliorate its effects. The ultimate effect of population persistence can be quite variable, depending on the complex relationships between short- and long-term cycles.
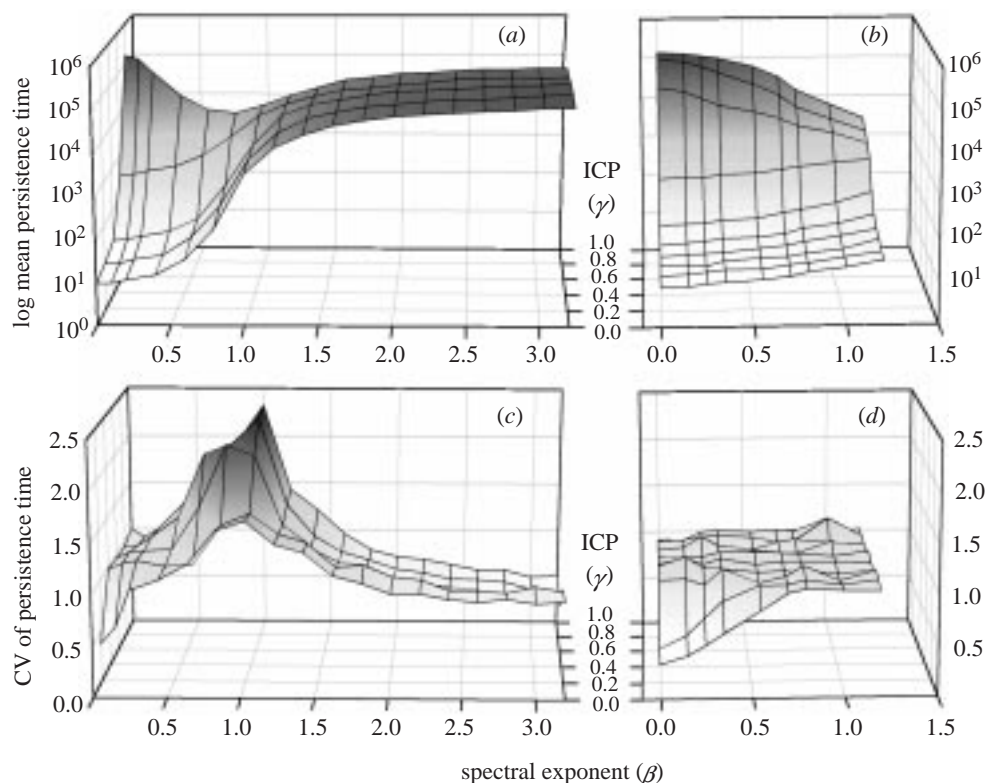
Figure 2. The effect of noise colour on log mean population persistence times and the coefficient of variation (CV) of persistence times for simulations using (*a*) and (*c*) a $1/f^{\beta}$ noise function and (*b*) and (*d*) an autoregressive noise function. The degree of over- or undercompensation is given by the intraspecific competition parameter (ICP) (γ), where $\gamma = 1$ indicates overcompensation. Noise colour (where noise has been incorporated in the carrying capacity) is indicated by the spectral exponent (β) and includes white ($\beta = 0.0$), red ($\beta = 1.0$), brown ($\beta = 2.0$) and black ($\beta = 3.0$) noise.

The unpredictability associated with red noise suggests that there is a fairly large probability that a population will become extinct in a short period of time, even when the mean persistence time is quite large. We define the probability of extinction as the percentage of populations that persisted for less than 100 generations. For populations with strongly undercompensatory dynamics ($\gamma = 0.2$), the mean persistence time decreases from white to red noise (white = 164 000 generations and red = 9800 generations) and the risk of extinction increases (figure 3*a* and 3*b*). There is an equal or slightly greater risk of extinction in a brown or black noise environment compared with a red noise environment (figure 3*b*–*d*), even though the mean persistence times are quite large (brown = 62 000 generations and black = 87 000 generations). However, there is a larger probability of persisting for a very long time (>100 000 generations) in a brown (76%) or black (77%) noise environment than in a red (29%) noise environment, suggesting that red noise environments are the most dangerous. For populations with overcompensatory dynamics ($\gamma = 1.0$), the mean persistence time increases several orders of magnitude with noise darkness (white = 10, red = 3400, brown = 78 000 and black = 124 000 generations), but for red noise there is still a high probability that a population will become extinct (figure 3*e* and 3*f*). Populations are unlikely to become extinct in the dark regions of the spectra (figure 3*g* and 3*h*).

Very simple autoregressive noise models are often used to incorporate the effects of reddened environmental variation (Mode & Jacobsen 1987; Ripa & Lundberg

1996; Johst & Wissel 1997; Petchey *et al.* 1997). Unfortunately, these models seem to be unsuitable for predicting the effect of noise colour on population dynamics where the underlying environmental variation is best described as a $1/f^{\beta}$ process. First- and second-order autoregressive models do not capture the unpredictability associated with red noise, nor are they able to simulate the darker noise colours present in some natural systems. Use of this technique may lead to an overly optimistic view of our ability to predict the effects of environmental noise on populations.

Our model incorporating $1/f^{\beta}$ noise suggests that populations are far more likely to persist for a very long time in a black noise environment than in a red noise environment. The probability of very short persistence times is either comparable to a red noise environment (strongly undercompensatory dynamics) or far less (strongly overcompensatory dynamics). Alarmingly, it appears that whatever the underlying population dynamics, the probability of extinction for a population exposed to red noise is quite large. In addition, we show that there is a large variation in the fate of particular populations exposed to red noise, suggesting that our ability to make accurate predictions regarding these populations is limited. We conclude that populations exposed to red noise should be considered more 'at risk' than populations exposed to black noise, and that more conservative management strategies should be adopted. Since environmental conditions exhibit a range of noise colours, there is clearly a need for more long-term studies that will allow us to evaluate
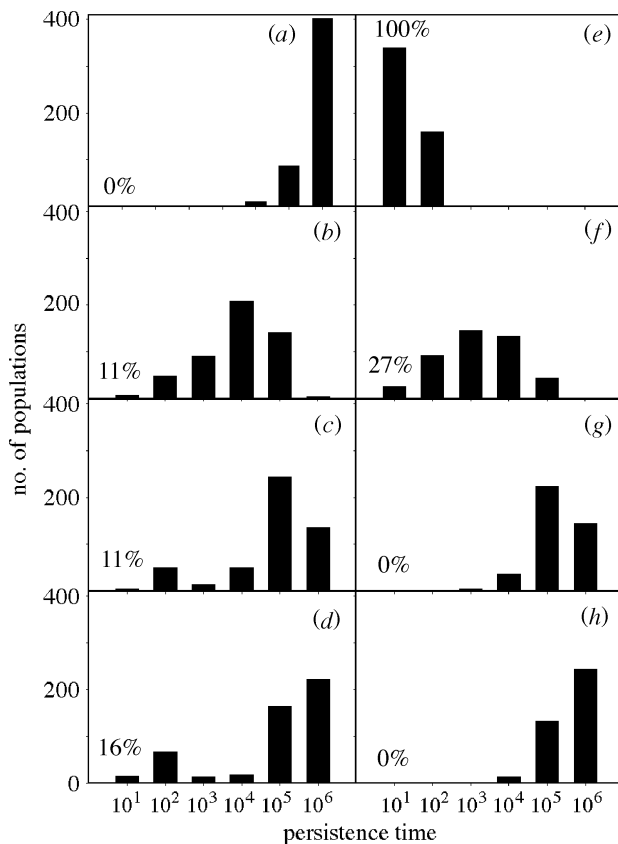
Figure 3. Histograms of population persistence time for models with (a)–(d) undercompensatory dynamics $(\gamma = 0.2)$ and (e)–(h) overcompensatory dynamics $(\gamma = 1.0)$ incorporating a $1/f^{\beta}$ noise function with (a) and (e) white $(\beta = 0.0)$, (b) and (f) red $(\beta = 1.0)$, (c) and (g) brown $(\beta = 2.0)$ and (d) and (h) black $(\beta = 3.0)$ noise. Percentages are the proportions of the populations that did not survive for more than 100 generations.

whether a particular population is being influenced by red or black environmental fluctuations.

REFERENCES

Halley, J. M. 1996 Ecology, evolution and $1/f$-noise. *Trends Ecol. Evol.* **11**, 33–37.

Halley, J. M. & Kunin, W. E. 1999 Extinction risk and the $1/f$-family of noise models. *Theor. Pop. Biol.* (Submitted.)

Hastings, H. & Sugihara, G. 1993 *Fractals: a user's guide for the natural sciences*. New York: Oxford University Press.

Johst, K. & Wissel, C. 1997 Extinction risk in a temporally correlated fluctuating environment. *Theor. Popul. Biol.* **52**, 91–100.

Kaitala, V., Lundberg, P., Ripa, J. & Ylikararjula, J. 1997 Red, blue and green: dyeing population dynamics. *Ann. Zool. Fenn.* **34**, 217–228.

Keshner, M. 1982 $1/f$ noise. *Proc. IEEE* **70**, 212–218.

Lande, R. 1993 Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**, 911–927.

Lapenna, V., Macchiato, M. & Telesca, L. 1998 $1/f^{\beta}$ fluctuations and self-similarity in earthquake dynamics: observation evidences in southern Italy. *Phys. Earth Planet. Inter.* **106**, 115–127.

Lawton, J. 1988 More time means more variation. *Nature* **334**, 563.

Lovejoy, S. & Schertzer, D. 1986 Scale invariance in climatological temperatures and the local spectral plateau. *Ann. Geophys.* B **4**, 401–409.

Mandelbrot, B. B. & Wallis, J. R. 1969 Some long-run properties of geophysical records. *Water Resources Res.* **5**, 321–340.

May, R. M. 1973 *Stability and complexity in model ecosystems*. Princeton University Press.

Mode, C. J. & Jacobsen, M. E. 1987 On estimating critical population size for an endangered species in the presence of environmental stochasticity. *Math. Biosci.* **85**, 185–209.

Pelletier, J. D. 1997 Analysis and modeling of the natural variability of climate. *J. Climate* **10**, 1331–1342.

Petchey, O. L., Gonzalez, A. & Wilson, H. B. 1997 Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. *Proc. R. Soc. Lond.* B **264**, 1841–1847.

Ripa, J. & Lundberg, P. 1996 Noise colour and the risk of population extinctions. *Proc. R. Soc. Lond.* B **263**, 1751–1753.

Saupe, D. 1988 Algorithms for random fractals. In *The science of fractal images* (ed. H.-O. Peitgen & D. Saupe), pp. 71–89. New York: Springer-Verlag.

Schroeder, M. 1991 *Fractals, chaos, power laws: minutes from an infinite paradise*. New York: W. H. Freeman & Co.

Steele, J. H. 1985 A comparison of terrestrial and marine ecological systems. *Nature* **313**, 355–358.

Vattay, G. & Harnos, A. 1994 Scaling behavior in daily air humidity fluctuations. *Phys. Rev. Lett.* **73**, 768–771.

Voss, R. F. 1988 Fractals in nature: from characterization to simulation. In *The science of fractal images* (ed. H.-O. Peitgen & D. Saupe), pp. 21–70. New York: Springer-Verlag.

Warner, S. C., Limburg, K. E., Arino, A. H., Dodd, M., Dushoff, J., Sterfiou, K. I. & Potts, J. 1995 Time series compared across the land–sea gradient. In *Ecological time series* (ed. T. M. Powell & J. H. Steele), pp. 242–273. New York: Chapman & Hall.